MÉMOIRES ET TRAVAUX DE L'IRAT
N° 3

# rice blast and its control

INSTITUT DE RECHERCHES AGRONOMIQUES TROPICALES

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SPREAD throughout the entire world, blast is one of the most serious diseases of rice ; in certain regions it is the key to high losses in yield.

In Latin America blast is present in every country, and today it is recognized as a major problem. In Brazil (57) – by far the biggest producer of upland rice on the continent – each year without exception blast rages particularly in the southern and central states. Although it is difficult to measure with precision, grain loss caused by blast has been evaluated under experimental conditions using a common variety : losses run from 17 to 52 % according to the intensity of the epidemic and it is estimated that they are in fact higher for the ordinary farmer. By controlling blast alone, Brazil could increase its annual rice production by two millions tons.

In Africa, identified as early as 1922 in Uganda, blast has only really developed in the course of the last fifteen years. It is now considered to be the main parasitic disease of upland rice in practically all of the rice-growing countries : Egypt, Senegal, Liberia, Ivory Coast, Upper Volta, Nigeria, Cameroon, Madagascar, to mention only a few. In the Ivory Coast the first very serious and destructive epidemic occurred in 1969 and since then blast appears every year with greater or less severity all over the country. In 1973 for example, in the north, certain varieties were destroyed up to 60 or even 80 % whereas the epidemic was less destructive in the western and central regions (16). In Nigeria, where blast was still regarded as negligible in 1969, since 1974 losses caused by blast equalled those attributed to brown spot (10-40 %).

In Asia where upland rice is cultivated on more than nine millions hectares, blast does not seem to attain a critical development in tropical climates except for certain regions known to be vulnerable. In India it appears seasonally in the plains and is endemic to the mountainous regions.

Caused by a fungus, *Pyricularia oryzae* CAVARA, the disease can affect all aerial parts of the plant.

On the leaves of susceptible varieties (blades and sometimes sheaths), small light spots appear first which then change into lesions of various sizes, brown, more or less circular, oval or spindle-shaped. Their centers become whitish or greenish grey (it is the fructification place of the fungus, and the « fuzzy » part contains the reproductive organs and the spores) ; they are often surrounded by a yellowish halo, zone of the progression of the necrosis. Leaf blast can start at any phase of tillering.

Blast attacks can also develop at the panicle level. Neck-blast manifests itself near the panicle node after flowering by a circular invasion. In extreme cases the neck breaks and the panicle falls over. The panicle racemes can be equally affected, which can also provoke partial sterility.

Neck and panicle blast are the ones that have the most disastrous consequences. However leaf blast provokes stunting of the plant, reduces the number of panicles, the weight of each grain and consequently the total weight of the harvest as well as its quality. If the disease occurs at the beginning of vegetation, the entire crop can be devastated, « burnt », and even disappears completely.

The intensity of the symptoms fluctuates greatly from one case to another ; this will depend on the interactions between the fungus, the variety, and the environment. Drought severely aggravates the circumstances and that is why research on the means of combating blast is one of the utmost importance for upland rice.

In most developing countries, although the use of chemicals is one means of blast control, the high cost and difficulties of application lead to its rejection or at least limit the possibilities for diffusion.

*1. Typical leaf lesions (Photo Notteghem)*

*2. Neck blast (Photo Notteghem)*

In fact, the use of varieties resistant to the disease is very widely recognized to be the most practical and economic to control blast, and the efforts of the researchers of the international community are aimed towards the obtention of such varieties.

# Varietal resistance to blast

Breeding for resistance to disease and in particular to blast, began in most research institutes right at the beginning of their programs for improving rice. Since it could be observed that during an epidemic varieties cultivated in the same place reacted differently, some being severely attacked, others to the contrary undergoing little or no damage, the practitioner recorded the degree of resistance or susceptibility in the varietal collections as well as in specific trials and bred for varietal resistance without really knowing its exact nature. The programs conducted in this manner generally led to the creation of varieties in which the resistance was overcome within a very small number of years.

The recent work of Van der Plank (64) (65) on resistance to diseases has brought to light the complexity and the plurality of the mechanisms implied and it was shortly after that better-founded breeding strategies began to develop. In the interest of simplification and because it is at the core of current research, for the essentials we will refer to Van der Plank's outline which distinguishes two forms of resistance called « vertical resistance » and « horizontal resistance » ; but we will also be led to make allusions to other concepts since the theories of this author are not admitted everywhere without certain restrictions.

This is extremely important in the sense that theoretical divergences lead naturally to different strategies for improvement which are, moreover, liable to be applied as well in the fight against other diseases or even against insects (31).

It seems useful to indicate briefly here a few general notions and definitions which will allow us to immediately situate the main points of the different types of resistance, concerning which we will then summarize the knowledge and breeding strategies.

We can distinguish monogenic resistance which is governed by only one gene (or « major gene »), identified, often even localized on a chromosome, and polygenic resistance, conferred by a certain number of genes (« minor genes ») of which only the combined effect is known. We can add to these an intermediate type where a small number of identified genes associate to give to the plant a type of resistance which is called « oligogenic ».

On the other hand, if we consider the fungus we must distinguish two types of pathogenicity. The pathogenicity of a given race includes virulence and aggressiveness. Virulence can characterize a race ; it expresses itself by a differential interaction with the variety, a virulent race attacks certain varieties and not others. Aggressiveness characterizes different strains of the same race ; it expresses itself without differential interactions ; a group of aggressive strains are always classified in the same order of aggressiveness on any variety.

Vertical resistance is specific, monogenic or oligogenic, characterized by differential interactions between the host and the parasite, and consequently is necessarily linked to the expression of virulence in the latter. A variety possessing vertical resistance is totally protected against certain races of the parasite, but is sensitive to others. This notion is accepted by all researchers ; it is sometimes designated by the term « specific resistance » or « true resistance ».

Horizontal resistance (or « general resistance ») is polygenic, and does not imply differential interaction between host and parasite. There is a link between horizontal resistance and aggressiveness because there is no difference between the effects of an increased horizontal resistance and those of a reduced aggressiveness (65). Horizontal resistance does not entirely preserve the plant from disease, but retards its development, whatever the strain or race of the fungus.

All varieties have horizontal resistance but to varying degrees. Certain plants have only this horizontal resistance ; others have vertical resistance as well. No plants have only vertical resistance (40).

The notion of « field resistance » found in japanese literature comes close to that of horizontal resistance although the two are not absolutely equivalent in the sense that in certain cases field resistance allows for control by a major gene and certain differential interactions. It is nevertheless defined as « what remains when vertical resistance has been eliminated » (18) (51).

« Slow blasting » designates, in Colombian works, the capacity of certain varieties to slow down pathogenic development (2) and refers to a point of view which is more epidemiological than genetic ; if it includes the other characteristics it can be assimilated to horizontal resistance.

# VERTICAL RESISTANCE

## Relationship between the plant and the fungus

In the system of vertical resistance in rice, for each gene that conditions resistance in *Pyricularia oryzae* there is a corresponding gene responsible for pathogenicity. This relationship places the rice-blast couple in the framework of the « gene-for-gene » theory worked out by Flor (19). In varieties of rice 15 resistance genes have been identified and the corresponding 15 virulent genes in the fungus (table I).

It is very likely that multiple resistance genes can be linked to a limited number of loci as Kiyosawa has demonstrated for the locus *k : Pi-k, Pi-ks, Pi-kp, Pi-kh* are allelic and located on the same locus but are different in their expression. This would tend to prove that other resistant genes could be identified (18).

To avoid any risks of ambiguity, let us pause for a moment to clarify the vocabulary. A resistance gene protects the variety against all the pathogenic races *which do not possess* the corresponding virulence gene. Thus it renders it resistant to all these races. However the variety remains susceptible to the races

*Table I* Varietal resistance genes and virulence genes of *Pyricularia* presently identified. (For the fungus the virulent state is indicated by +).

| Locus | Resistance gene of the variety | Virulence gene of *Pyricularia** |
|---|---|---|
| a | *Pi-a* | $Av\text{-}a^+$ |
| b | *Pi-b* | $Av\text{-}b^+$ |
| i | *Pi-i* | $Av\text{-}i^+$ |
| f | *Pi-f* | $Av\text{-}f^+$ |
| k | *Pi-k* | $Av\text{-}k^+$ |
| | *Pi-kh* | $Av\text{-}kh^+$ |
| | *Pi-kp* | $Av\text{-}kp^+$ |
| | *Pi-ks* | $Av\text{-}ks^+$ |
| m | *Pi-m* | $Av\text{-}m^+$ |
| ta | *Pi-ta* | $Av\text{-}ta^+$ |
| | $Pi\text{-}ta^2$ | $Av\text{-}ta^{2+}$ |
| t | *Pi-t* | $Av\text{-}t^+$ |
| z | *Pi-z* | $Av\text{-}z^+$ |
| | *Pi-zt* | $Av\text{-}zt^+$ |

*Remark : the gene Pi-m was localized at the locus Pi-k and a more recent designation is Pi-km (Kiyosawa, 1978).*

possessing the virulence gene in question and only to these races. For example, a rice variety having the resistance gene *Pi-k* is resistant to all the races of the fungus where the gene *Av-k* in a virulent state is not found. It is susceptible to races which possess it.

This can be expressed in other terms : if a variety has only one vertical resistance gene, *Pi-k,* the only virulent gene the fungus needs to succeed in causing an infection is $Av\text{-}k^+$. Thus the gene of the variety said to be « resistant » appears in fact as a factor of exclusive susceptibility.

## Identification of fungus races and varietal resistance genes

To study the possibilities of using vertical resistance for varietal improvement, it is indispensable to know on the one hand the fungus, that is the races comprising the population dealt with, and, on the other hand, the genotype of the varieties from the point of view of their resistance.

## Recognizing the races of the fungus : differential varieties

Since all the combinations of virulence genes are susceptible to appear in fungus populations, we can, in theory, identify $2^{15}$ races. In the Philippines, more than 300 races have already been recognized (52).

To identify races of *Pyricularia oryzae* present in a population, we take a sample of strains from diseased plants which we use to inoculate a group of varieties where each has a different vertical resistance gene from the others, or « differential variety set ».

Since two varieties are differential if they react differently to a same race of fungus, they permit us to theoretically establish a distinction between four races ; four varieties can discriminate sixteen races ; *n* varieties $2^n$ races. The greater the number of varieties of a set, the greater, consequently, will be the number of races susceptible to being recognized. Japanese research workers (18), the first to set up a differential set emphasize that each variety must possess one and only one major resistance gene.

If such is the case, and to take only one theoretical example, a race having the virulence genes *Av-a, Av-k, Av-z,* inoculated on eight differential varieties possessing respectively the resistance genes *Pi-a, Pi-b, Pi-i, Pi-k, Pi-kh, Pi-m, Pi-ta, Pi-z,* would produce lesions on only three of them (*Pi-a, Pi-k, Pi-z*), and would leave the five others totally unaffected.

In fact in certain sets we find some varieties uniting two or even three resistance genes, which renders identification more delicate.

An ideal set of differential varieties could be chosen by taking successive steps in the following manner (32) : choice of provisional differential varieties ; choice of provisional differential fungal strains ; genetic analysis of the varieties ; selection of new differential varieties based on the « gene-for-gene » theory.

Numerous countries have worked out a differential set of varieties : Japan, U.S.A., Taïwan, Philippines, India, Korea, Columbia...

By way of example, here is the differential set adopted by Japan in 1976 (37). It is composed of nine varieties with the resistance gene in parentheses : Shin 2 (*Pi-ks*), Aichi-Asahi (*Pi-a*), Ishikari-Shiroke (*Pi-i*), Kanto 51 (*Pi-k*), Tsuyuake (*Pi-m*), Fukunishiki (*Pi-z*), Yashiro-Mochi (*Pi-ta*), Pi No. 4 (*Pi-ta²*), Toride 1 (*Pi-zt*).

However it is difficult to compare the races of a parasite identified in one country using a particular set with those of another country based on another set. This is where the need for an international set comes in, in order to facilitate exchanges of information and comparisons of results. According to Kiyosawa (32) an ideal international set of differential varieties should be chosen among differential varieties selected in various countries after their genetic analysis. In 1967 an international set of eight varieties was adopted, finalized conjointly by Japan and the United States, which permitted identification of $2^8 = 256$ strains as well as a standardized coding system of these « international races », divided into 32 groups (51). In the tests of the International Rice Blast Nursery (IRBN), several sets, or only parts of them, are used as a complement to the international set. No.

matter what, the multiplication of trial sites should favor comparisons of the different sets.

### Recognizing varietal genotypes : differential races of *Pyricularia*.

Just as the races of a fungus can be identified only by the intermediary of differential varieties, so it is that only by observing the reaction of a variety to a set of known races of a fungus can we determine that or those resistance genes which the variety may possess.

An ideal differential set of *Pyricularia* would be composed of either races where each one has only one avirulence gene, or races where each one has only one virulence gene. Now it is certainly not easy to put together such a set : most of the races collected in the field have numerous avirulence genes ; it is easier – but very relative – to find races having only one virulence gene, each one of them attacking only one differential variety (32). IRAT (23) reports that it has not yet been possible to obtain a set of natural differential races of *P. oryzae* originating in Africa because of the high frequency of a virulent state for certain genes in the strains studied. However this is not the case in all rice-growing situations and it appears that Asian researchers encounter less difficulty in this domaine. Moreover most researchers have difficulty maintaining the stability of the pathogenicity of the races under culture (cf. *infra*). Only Japanese researchers seem to have at their disposition material of relatively low variability (37).

Just as the races of *Pyricularia* likely to being determined depend on the differential varieties used, the resistance genes which can be detected in the varieties depend on the extent of the set of the differential races of the fungus.

In Japan, Kiyosawa having selected seven races of *Pyricularia* had determined by an iterative procedure twelve representative varieties based on their reaction to these races : for example the variety Aichi-Asahi represented a type having the *Pi-a* resistance gene, and the variety Ishikari-Shiroke a type having the *Pi-i* gene, etc. By comparison, 397 varieties had been classified into twelve groups. Other Japanese researchers using supplementary differential races have since shown that Kiyosawa's classification could be refined. Thus the type Kanto 51 which, according to Kiyosawa possessed the *Pi-k* resistance gene, was subdivided into three genotypes : *Pi-k ; Pi-i Pi-k ; Pi-k Pi-m* (51). None of the new systems of classification differs essentially from that of Kiyosawa and thanks to this method most varieties of rice cultivated in Japan as well as numerous varieties of local origin could be systematically studied and classified for their vertical resistance : the resistance gene(s) which each variety possesses are known with, however, this restriction, that the test with the aid of new races could, in certain cases, reveal additional resistance genes.

It would seem that because of the difficulty of putting together complete natural differential sets of *Pyricularia* researchers are resorting more and more to mutagenesis, either physical or chemical. It is easier to create virulent races from avirulent ones (41). The mutants obtained are screened on differential varieties and complete artificial sets of virulent races have been set up in this manner.

### Evaluation of the symptoms

Whether we want to determine the races of *Pyricularia*, know varietal genotypes to use them for selection, or evaluate newly created varieties, we observe the same phenomenon : the presence or absence of lesions on plants subjected to contamination, from which we infer both the host's resistance and the pathogenicity of the parasite. Whatever the final objective may be, the environmental conditions must be such that the strongest possible infestation can develop (49), so there is no risk of the epidemic « forgetting » varieties which should be affected. In particular cultivation must be undertaken under rainfall conditions but while maintaining a very humid microclimate, and with intensive use of nitrogen fertilizer. It is often admitted by certain researchers, but contested by others, that the symptoms observed on the seedling reflect those which one will find at the last stages of development, and that is why young plants are observed. Experiments are done, depending on the case, either in field nurseries or under artificial conditions. However the correlation between leaf and neck blast has not always been demonstrated.

With natural contamination in the field we can study both varietal reactions to the local complex of *Pyricularia* and its components using sets of differential varieties. The experimental device has been standardized so that international programs could be set up (International Uniform Blast Nursery Programme) (49). The varieties are planted side by side, closely together in short lines, and are surrounded by a large strip of a very susceptible variety (spreader) acting as the supplier of the inoculant of *Pyricularia oryzae*. In these trials the plants are exposed to all the races of the fungus present on the site throughout the test. Since the races evolve from one season to another – as we shall see further on – the tests must be repeated so that varietal reactions to all the existing races on the site can be observed. Cross-checking the results obtained on various sites enables us to get a picture of the resistance of each variety.

Nevertheless, certain studies can only be carried out under controlled conditions : such as, for example, the examination of varietal reaction to specific races of the fungus. These trials take place in the greenhouse or sometimes in humidity chambers. Inoculation is carried out artificially either using a syringe or by spraying spores on the plants (21). Whatever the case, under conditions so far from those of natural infestation, we cannot hope to obtain a precise picture of rice resistance in the field (47).

The evaluation criteria to the reaction of the infection are essentially qualitative : height, form, color, that is, type of lesions appearing on the leaves after six days ; certain researchers add quantitative criteria : number of lesions per leaf or per unit leaf area and number of leaves completely destroyed. The sign of vertical resistance is a complete « refusal » of the development of lesions ; hypersensitive reactions are included in the same category (14) and are characterized by brown spots without sporulation (the virulent fungus destroys the first cells so rapidly that it cannot spread further).

Several evaluation scales based on these criteria have been developed. Certain designate the type of reaction by numbers (1, 2, 3, 4, 5, etc.), and others use symbols (b, bg, bG, pG), or letters (A, B, C, D, E).

One of the most frequently used methods of scoring is Kiyosawa's. Here is an adaptation used by IRAT in the Ivory Coast. There are 6 degrees (47) and their correspondence with Kiyosawa's scale is given in parentheses (34).

- 1 No symptoms or apparent discolorations
- 2 Numerous brown spots (brown spot = b)
- 3 Brown lesions with differentiated center of less than one mm in diameter (brown grey = bg)
- 4 Brown lesions with a differentiated center of less than two mm in diameter (brown Grey = bG)
- 5 Brown lesions with a differentiated center of more than two mm in diameter brown Grey = bG)
- 6 Big grey lesions with purple margins (purple Grey = pG)

In theory, vertical resistance gets a score of 1. In reality, lesions corresponding to scores of 2 and 3 sometimes appear to be vertical-type reactions. We consider that scores from 1 to 3 characterize resistant varieties and avirulent races, scores from 4 to 6 characterize susceptible varieties and virulent races. A big difference between the minimal and maximal score is a sign of vertical resistance of a variety inoculated with differential races.

In the standardized system developed by IRRI for the international rice testing program, the scale for blast has nine grades of which the first four refer to the type of lesions, and the other five to the percentage of the leaf area affected with typical lesions ; the two categories of criteria can be combined (26).

The identification of symptoms of vertical resistance is not quite as simple as one may imagine from reading the foregoing, and recognition of the virulence genes of a race is not always easy.

In practice, under natural as well as artificial conditions, most of the time we can observe a juxtaposition of a variable number of spots of different types on the same leaf. Often the breeder takes into account only the predominant type of lesions and attributes only one score to the variety, thus neglecting a factor which could be important, that is heterogenic lesions expressing a heterogeneity in the fungus population.

On the other hand, the expression of symptoms on a set of differential varieties is subject to variations resulting from three types of factors : differences, already mentioned, due to the method of inoculation ; loss of aggressiveness of races of *Pyricularia* when they are preserved *in vitro* and to which it is then necessary to give back their original vigour by different techniques ; finally, factors inherent to the very set of differential varieties which bring up the problem of improving the representativeness of certain sets since the symptoms are not always clear and easily interpreted.

## Selection for vertical resistance

Endowed with a unique gene or a very small number of genes, vertical resistance is relatively easy to breed which explains its frequency in the varieties created by Research Institutes.

As far back as 1942, Japanese researchers (18) introduced in their varieties major resistance genes of foreign origin. Today this is what we call « vertical » resistance. From then on they sought, like researchers in other countries, other very resistant varieties to serve as parents, among the different types of rice, *indica* or *japonica*. However, considering the genetic diversity of rice, it is astonishing to note the small range of parents used world-wide. A table (18) indicating the sources of resistance used in Japan in 1972 shows only twelve varieties containing in all seven resistance genes. Certain varieties are constantly being cited in literature, for example, Tadukan, Tetep, Zenith ; they are used in India and Columbia as well as in Japan and even sometimes in Africa. This leads certain authors to suggest the search for new sources of resistance (10).

These varieties, whose rôle is to bring in a very specific resistance gene capable of confronting locally identified races of the fungus, are crossed with varieties possessing good agronomical characteristics : high yield, good grain quality, etc. The hybrids are then backcrossed with the high yielding parents.

Resistance tests allow us to select the best progeny. All the improvement programs opting for the use of vertical resistance have succeeded in creating numerous and excellent varieties totally unaffected by the disease.

Unfortunately, the blast resistance of the new varieties is far from being a definitively acquired characteristic. In 1979 a Japanese author (18) wrote : « *The breakdown of true resistance was really unexpected and shocking for Japanese breeders and plant pathologists* ». One after another the resistant varieties became susceptible again only a few years after their release practically all over the country. The most striking cases were those where a field planted with a variety reputed to be resistant was observed next to one where a local susceptible variety was being cultivated : the « resistant » variety was often more severely affected by the disease than the susceptible one. The same phenomenon was described in other countries in Asia, South America, and Africa on a great number of varieties.

These observations were made on irrigated and upland rice. A variety such as SE 302 G created in Senegal and cultivated in upland conditions, formerly resistant in the breeder's field, is now susceptible in the fields of the common farmer (43).

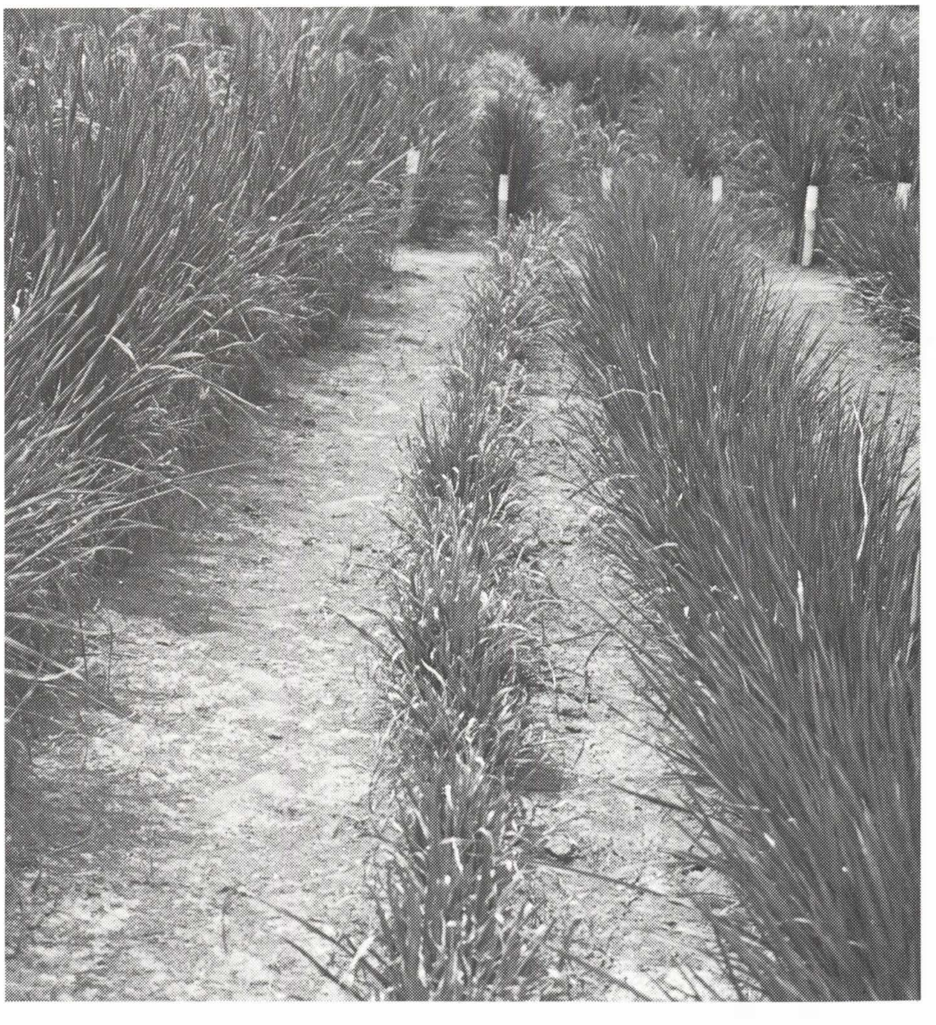
## Causes of instability of vertical resistance : fungus variability and selection pressures

Where did these failures come from ? Samples of the parasite are collected from diseased plants and their pathogenicity is tested on differential varieties. We discover then that new races of the fungus have propagated, precisely those races against which the varieties concerned, having vertical i.e. specific resistance, were not protected.

This new situation is the result of pressures which the plant and the fungus undergo and exert, and of the considerable capacity for transformation (variability) of the latter.

The potential for variability of *Pyricularia oryzae* is manifested in certain of its characteristics but especially – and it is this that interests us – in its pathogenicity. We find not only very numerous races in rice growing zones, several races within the same population, but moreover it has been put forward that isolated cultures of conidia born of a unique lesion, cultures coming from only one conidium and even cultures from the cells of a conidium, could all produce different forms of virulence (52). The truly exceptional extent of this phenomenon of variability could perhaps be attributed, according to certain researchers, to a variation in the number of chromosomes of the conidial cells (52), it could also be provoked by mitotic recombinations and mutations, moreover these different mechanisms may well add up with each other. We must note however that all authors do not arrive at such clear conclusions on the question of pathogenic variability of the fungus (37).

*3. A susceptible variety line between two resistant varieties (Photo Seguy)*



*4. Trial plots showing blast resistant and susceptible varieties (Photo Bidaux)*

An experiment conducted by IRAT (4) on a strain in the Ivory Coast, Danane, having numerous known virulence genes : *Av-a, Av-i, Av-zt, Av-b, Av-f, Av-z, Av-kh, Av-k,* has shown that these genes, present at the beginning in the strain, are found again unchanged after 15 asexual generations. Thus the genes *Av-a, Av-i, Av-zt, Av-b, Av-f, Av-z, Av-kh, Av-k,* do not seem to mutate with high frequency.

A selection pressure called « directional » is imparted by the variety possessing a vertical resistance gene to the population of *Pyricularia* ; this pressure acts in exclusive favor of the races present in the population which are virulent for the variety.

Let us assume that in a given region, within the *Pyricularia* population, the races having the *Av-k* virulence gene are present in only minute quantities and have not been detected by tests on differential varieties, or are even non-existent (but can appear). We then plan to cultivate a variety possessing the corresponding *Pi-k* resistance gene which protects it against all the other races present. This is where the races carrying the *Av-k* virulence gene, the only ones to which the variety remains susceptible, begin to proliferate ; enjoying a selective advantage, within several years they come to make up practically the total parasite population. Henceforth the varietal resistance gene becomes ineffective, the variety becomes susceptible and we must begin all over again.

The breakdown of vertical resistance, commonly observed within two to six years and sometimes as early as the first year, occurs even more rapidly when the variety is cultivated uniformly over great areas. This is what Van der Plank (65) calls « the price of the popularity of a variety ».

Theoretically however, another. pressure is exerted in the opposite sense, this time by the environment. This is the « stabilizing » pressure which tends to cause a decrease in the races possessing superfluous virulence. This mechanism can be triggered as soon as the directional pressure of the variety stops : for example, between two harvests of the resistance variety, or if the fungus can infect other species or susceptible varieties. The strains carrying useless genes are at a disadvantage. However, the stabilizing pressure does not act on all the useless virulence genes with the same intensity ; certain genes called « strong » are highly at a disadvantage, while the « weak » genes are less so. The corresponding resistance genes in the varieties are also called strong and weak.

Does this process, favorable to the plant, really occurs in the case of rice and blast ? Do the races in which virulence is no longer necessary during the absence of the resistant rice variety diminish or disappear ?

Chevaugeon et *al*. (12) measure indirectly the loss of competitiveness of the race of a fungus carrying a useless virulence by placing it in competition with a non virulent race in conditions where this virulence is not necessary.

In one experiment they compare three lines of *Pyricularia oryzae* differing in their virulence factors on two varieties of rice (table II).

The couple 111-P2 is put in competition on the variety K2. The variety Aichi-Isahi is inoculated with the 125-P2 couple.

The conidial production of each of the clones measured in the course of several successive infectious cycles confirms that the elements of a parasite population are all more at a disadvantage, the more they differ from the genetic structure just necessary to overcome the vertical resistance of the host variety.

Here in fact, the line 111 of *Pyricularia oryzae*, which has only one useless factor to provoke lesions on the variety K2, is more competitive than the line P2 which has nine factors. The line 125, which carries the biggest burden of useless factors, is the least apt to survive.

*Table II* Comparison of three *Pyricularia oryzae* lines on two rice varieties.

| | | Factors of virulence in *P. oryzae* and of resistance in rice | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *P. oryzae* lines | 111 | *Av-a*$^{+}$ | *Av-kp*$^{+}$ | *Av-kh*$^{+}$ | | | | | | | | | | |
| | P2 | *Av-a*$^{+}$ | *Av-kp*$^{+}$ | *Av-kh*$^{+}$ | *Av-b*$^{+}$ | *Av-i*$^{+}$ | *Av-f*$^{+}$ | *Av-k*$^{+}$ | *Av-ks*$^{+}$ | *Av-t*$^{+}$ | *Av-z*$^{+}$ | *Av-zt*$^{+}$ | | |
| | 125 | *Av-a*$^{+}$ | *Av-kp*$^{+}$ | *Av-kh*$^{+}$ | *Av-b*$^{+}$ | *Av-i*$^{+}$ | *Av-f*$^{+}$ | *Av-k*$^{+}$ | *Av-ks*$^{+}$ | *Av-t*$^{+}$ | *Av-z*$^{+}$ | *Av-zt*$^{+}$ | *Av-ta*$^{+}$ | *Av-ta*$^{2+}$ |
| Rice varieties | K2 | *Pi-a* | *Pi-kp* | | | | | | | | | | | |
| | Aïchi-Asahi | *Pi-a* | | | | | | | | | | | | |

When the lines P2 and 125 are put into competition they behave in the following manner : the relative proportion of P2 in the mixture doubles in 1.43 passages on the variety of rice Aichi-Asahi while that of the line 125 decreases by half in the same time. They differ only by the presence of two supplementary useless factors, *Av-ta* and *Av-ta*$^2$ in the line 125. One of the two genes *Pi-ta* or *Pi-ta*$^2$ (or both) could be « stronger » than the eight others, *Pi-b, Pi-f, Pi-i, Pi-k, Pi-ks, Pi-t, Pi-z, Pi-zt*, corresponding to the useless virulence genes.

Aside from the cases of the genes *Av-ta* and *Av-ta*$^2$ whicn were strong in the Ivory Coast (7), and *Av-z* which is sometimes strong (4), the stabilizing pressure generally seems much less efficient than the theory would have it in the case of rice blast. However the longevity of vertical resistance depends largely on this since it is opposed to « directional » pressure which itself favorizes the most virulent races of the pathogen for the variety cultivated.

## Strategies for the use of vertical resistance

To summarize the preceding, we can say that the vertical resistance of a variety of rice induces or at least allows preferential proliferation of the races of *Pyricularia* virulent for it in the zone where it is cultivated.

Avoiding the moment when this virulence becomes dangerous, or trying to prevent its outbreak, are the bases for the various strategies of combat using this type of resistance.

### Accumulation of genes

The technique called « pyramiding » consists of the cultivation of a variety possessing first only one resistance gene and incorporating into it, each time that it becomes susceptible again, a new gene protecting it against new races. This procedure, repeated a number of times, results in an accumulation of resistance genes in the same variety (14).

At first glance, this technique is agronomically very attractive since as long as the last resistance gene introduced has not been overcome by a new race of the fungus, the varieties are totally unaffected by disease. But we can easily imagine that this implies a veritable competition between the parasite and the breeder, and could only function in countries with adequate infrastructures for warning and agronomic research, and efficient production and distribution of seeds. It would be difficult to base the chances for improving the varietal resistance of rice on such a strategy in developing countries which never have the required structures.

Along the same line, researchers (18) propose the simultaneous accumulation of numerous resistance genes in a kind of « super-variety » which would be resistant to all or most of the existing races of the fungus. The transfer of all these genes obtained by polycross would come up against the difficulty of identifying those really acquired by the hybrids. It would seem that the higher the number of genes likely to be introduced, the less numerous are the available races of the fungus for testing their presence. Thus Japanese researchers do not have races of

*Pyricularia* allowing them to distinguish a plant carrying four genes, *Pi-a, Pi-k, Pi-i,* and *Pi-z*, from a plant having only three, *Pi-a, Pi-k, Pi-z* (18).

Another recently devised strategy (18) is based on the observation of the very large spectrum of the vertical resistance of certain varieties such as Tetep or Carreon, and of the very high variability of the fungus. In this case, the pressures of selection would not be active. According to this theory, as many cross-breedings as possible could be undertaken among highly resistant varieties and only those hybrids showing the highest resistance level in the field, which would correspond to the greatest accumulation of genes, would be conserved. It would not be necessary to identify the gene one by one. Only a few lesions could form on plants having such resistance, even if an assortment of « super-races » of the fungus appeared. Consequently this resistance would have a character of stability and would be apparently similar to horizontal resistance.

Whatever the case, we must emphasize that the transmission of vertical resistance is rarely total. Thus an upland variety very resistant to blast in Japan, Sensho, was often used as a parent, but its progeny have never been as resistant. The same phenomenon can be observed in Columbia with Tetep (51).

## Composite varieties or multilines

A composite variety is formed by a mixture of seeds from two or more lines, each one differing from the others only by a strong gene for varietal resistance.

Each line exerts a directional selection pressure which favorizes the races possessing the corresponding virulence gene, but on the other hand, the races having useless (ineffective) genes are at a disadvantage. For the composite to be fully efficient, the lines must be dosed in such a way that each race has the same probability of encountering a susceptible host. We must therefore take into account the estimated or desired frequency of the pathogen population (5) in a state of equilibrium.

This strategy would consist in regrouping the most possible monogenic resistances with the implicit hypothesis, here too, that this collection would behave in the same way as if found in the presence of a horizontal resistance or of a polygenic control (14). Thus we could avoid the defect of varieties with vertical monogenic resistance whose cultivation over big areas lies at the origin of a unique pressure in favór of the same races.

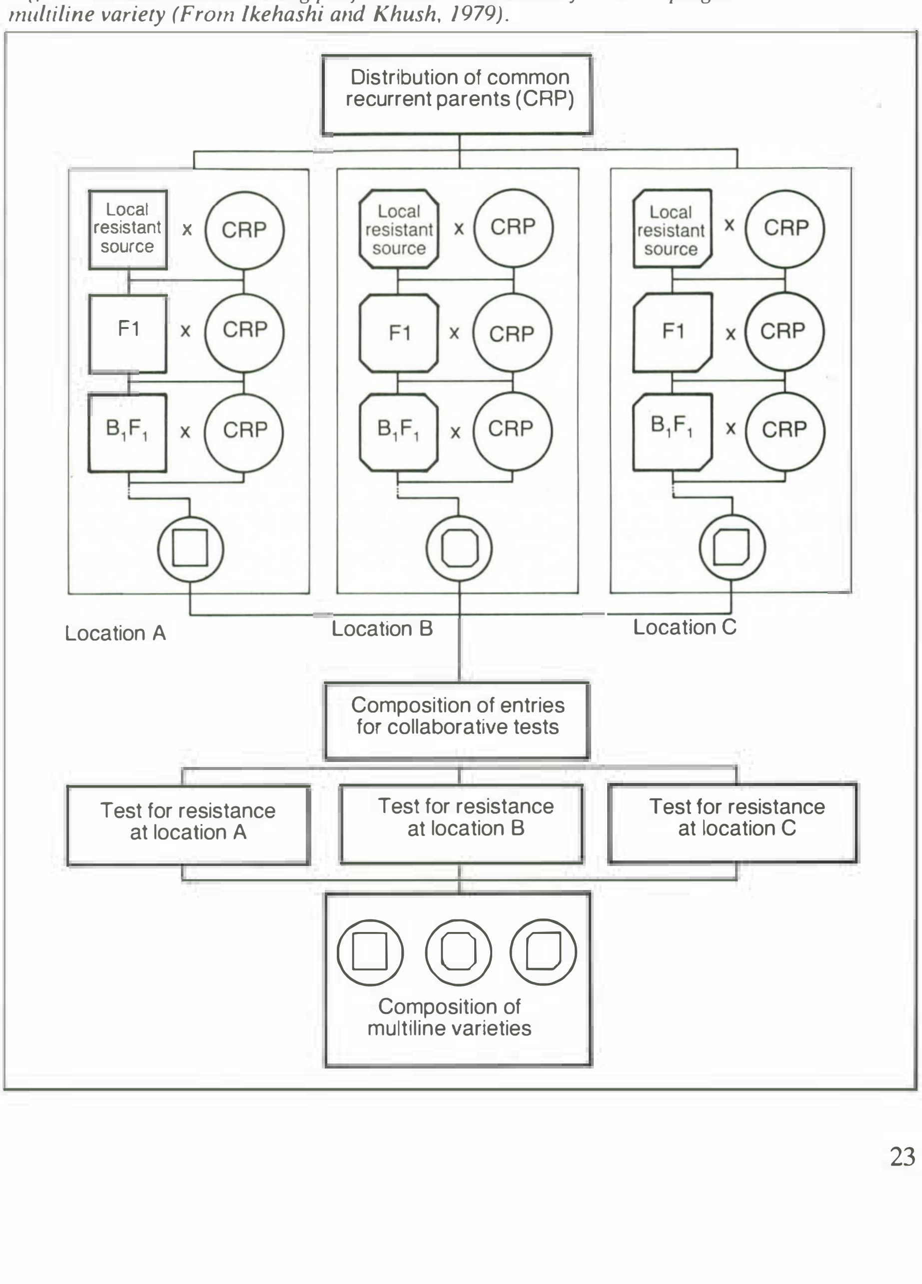
Another advantage of composite varieties is the supplementary protection offered by the phenomenon of hypersensitivity. A potential site of infection that is attained by a spore without the necessary virulence, reacts by setting up very strong defence mechanisms. The induced defence system protects the potential site, for at least some time, against the installation of a virulent race. The phenomenon of cross protection is all the more efficient when the pathogen population is made up of a greater number of races with different virulences.

Here and there, certain observations or criticisms have been formulated with regard to composite varieties.

Let us recall first that « strong » resistance genes do not seem very numerous. The risk of the rapid appearance of a virulent strain of the parasite with regard to all the composing lines (14) has also been cited, but we object to this that the races having the best parasitic fitness are those which have the least useless virulence genes and that it would not be possible for a super-race to invade the fungus population (5). Moreover producing series of almost isogenic lines is not very easy.

IRRI (20) proposes a procedure with international collaboration : resistant parents are bred in different research centers and are used in as many programs of back-crossing with one (or several) common recurrent parent(s), possessing the desired agronomical characteristics. After 5 or 6 back-crosses, the isogenic lines are ready to be mixed to form the composite variety, except for the characteristic of vertical resistance (fig. 1).

*Fig. 1 Collaborative breeding project on blast resistance for developing a multiline variety (From Ikehashi and Khush, 1979).*



Let use note however that the effectiveness of the use of composites in combating blast is debatable. Certain authors affirm that this strategy truly constitutes a means of slowing the epidemic (18), whilst others think that its potential advantage over varieties with vertical monogenic resistance remains to be proved (51). It is true that breeding programs including the creation of composites are only beginning and at the present time only few results are available for evaluation.

### Varietal rotation

Here again it is a question of avoiding preferential proliferation of virulent races for the crop, but this time by associating an agronomical intervention with genetic resistance.

Since remote times peasants have practiced species rotation and within the species, varietal rotation, in order to overcome disease, among other reasons. Today for example, Philippino farmers commonly rotate rice varieties simply because they have noted that the attacks of the disease were less violent than when the same variety is used over and over (14).

The efficiency of this empirical practice can be easily explained by the concepts developed above : the races of pathogen present in a given zone depend on the varieties cultivated there ; their evolution is directly linked to the resistance genes carried by the varieties. We can suggest a rotation of varieties having different resistance genes, removing variety A from cultivation just before its resistance breakdown, and replacing it with variety B, which will then be replaced by variety C, etc. with a possible return to variety A (29). Such a strategy requires a perfected system for seed production and distribution, efficient supervision of the farmers, and finally prediction of the evolution of the races or of the longevity of the vertical resistance, which amounts to the same thing. However, although mathematical formulas have been worked out to determine this longevity (5), their accordance with reality has not been demonstrated and certain authors are not far from considering strategies based on this type of prediction as unrealistic (37). Finally, we cannot completely exclude the possibility of the appearance of a « super-race » virulent to all the varieties of the series if the mechanisms of stabilizing selection cannot be brought into play (18).

What is to be thought of the use of vertical resistance in the case of rice blast ?

Although this form of resistance is the best-known, many points concerning genetics and the relationship between host and parasite need further study. For this approach there are still many methodological problems.

From a practical point of view, varieties with vertical resistance can be misleading if used inconsiderately. Totally healthy for one, two or three years, they will suddenly be ravaged by the disease. That is why different strategies are being worked out using the strong points of each. The application of certain strategies appears relatively simple, others, on the contrary, face important technical difficulties. At the present moment, researchers have not yet given their consensus to any one among them, but each strategy could, without doubt, be beneficial in certain situations.

We will emphasize here once again that none of these strategies can be put to work outside of a high level agricultural situation ; it is not by chance that Asian countries (particularly Japan) have studied vertical resistance, and if in developing countries – particularly Africa – we have turned towards other types of resistance, less spectacular, but more viable in still less-evolved agricultural contexts.

# Horizontal resistance

## Why breed for horizontal resistance ?

Another model, not excluding vertical resistance but using other mechanisms, was proposed by Van der Plank (64) (65) following observations on diverse crops. It was taken up again by Robinson (59) and discussed by, among others, Parlevliet and Zadoks (53) (54) : horizontal resistance.

In this model specific genetic links do not intervene in the host-parasite relationship : a variety behaves identically to all races ; the races of the fungus always express their aggressiveness on various varieties in the same order. An undetermined number of genes govern this type of resistance in the plant. They act on various characteristics, anatomical, physiological, and biochemical, which have not been completely determined, and which lie outside of the possibilities of variation of the parasite. This resistance is permanent.

What must be underlined, according to Robinson, is not so much the fact that this resistance is polygenic, contrary to vertical resistance which is monogenic, but the fact that the genes involved are of a different nature : thus vertical resistance and horizontal resistance seem to be different characteristics that can work together, the latter always existing, even at a very low level.

However, for Parlevliet and Zadoks (53) the two types of resistance are of the same nature, there is a gene-for-gene relationship with the parasite in both cases, but the genes responsible for what is called horizontal resistance (minor genes) are numerous and it is the polygenic aspect of one, and the mono – or oligogenic – aspect of the other which make the difference. The total action of the resistance and virulence genes is situated in an integrated system where major genes, rare, have important or easily identifiable effects (vertical resistance), and minor genes, more frequent, have less effects still poorly defined, but which probably add on, one to the other, (horizontal resistance).

Faced with numerous horizontal resistance genes of a variety, the pathogen population would have more difficulty adapting and making the necessary genetic transformation to reach a high level of aggressiveness ; in this case the phenomenon of genetic homeostasy, which tends to maintain the parasite population in its genic composition, would come into play more strongly than in a monogenic situation characterizing vertical resistance. Thus an explanation for the stability of horizontal resistance.

Shortly thereafter, Parlevliet (54) completes his theory by also admitting a form of horizontal resistance which does not imply a relationship between the genes of the host and those of the parasite. This resistance, called escape resistance, operates by reducing the risks of contact between host and parasite, and often depends on morphological characteristics of the plant.

Thus definitively, according to this author, horizontal resistance can fit in with either a polygenic model but with a gene-for-gene relationship between variety and parasite, or with a model where this link is nonexistent.

Taken in the wider sense of a lasting resistance, without taking into account divergences in theorical interpretation, is the model of horizontal resistance admissible in the case of rice and blast ?

On the side of the disparagers, Crill and *al.* (14) without refusing a hypothesis of controlled resistance by a polygenic mechanism affirm that, sensitive to the environment, it becomes inefficient when the conditions are favorable for triggering an epidemic and especially in the case of upland rice. To count on this resistance only appears dangerous and foolhardy.

S.H. Ou, another pathologist of IRRI, more categorical, affirms in 1979 in a critical review (51) that no rice variety possessing horizontal resistance has been identified.

Yet the hypothesis of horizontal resistance really seems to have been verified.

Since 1972, only a few years after the publication of the Van der Plank theory and while blast was spreading dangerously in Africa, IRAT has been working in this direction. Although horizontal resistance presents, since the beginning, because of its nature, a lot more problems to the scientist than vertical resistance, the fact that is was described as durable was sufficient to make it very interesting, especially in the context of developing countries. Yet it was necessary to have the certitude that exist for rice cases of stable resistance which means varieties which could be used as sources of horizontal resistance. Thus during their breeding work in tropical regions IRAT scientists had frequently noticed among traditional upland rice varieties from Africa and Latin America and certain Asian regions a high level of resistance to blast and the maintenance of this resistance overtime (30).

African upland rice varieties like Moroberekan, 63-104, R 75, RT 1031-69, LAC 21, LAC 23 and Brazilian varieties Dourado Precoce and Iguape Cateto have been resistant to blast for more than ten years. Varietal resistance created from the afore-mentioned by mutation or hybridation like IRAT 13, IRAT 104, IRAT 112, seem to be of the same nature.

Until proven to the contrary these varieties possess stable resistance. Moreover genetical studies on a few of them have shown that their resistance is not monogenic. These characteristics are those of horizontal resistance (46).

The observations by IRAT agree with those of Japanese scientists (18), who after bitter disappointment over vertical resistance, have looked for field resistance among their varieties. This type of resistance is very close to horizontal resistance because most of the time it results from a polygenic system and does not induce specific reactions to fungus strains. Among the varieties retained after experimentation some of them have been cultivated by Japanese farmers for many years with good results.

Horizontal resistance expressed in epidemiological terms by retarding and low level of development of blast resulting from several phenomena the most evident of which seems to be : a longer incubation period (or latency), a reduction in the quantity of spores produced by the lesions, a lower percentage of spores succeeding in infection. Important varietal differences in the capacity for retarding the development of the lesions have been observed (44) (66) and that is a factor which has to be studied in the search for resistant varieties. In spite of these different phenomena, the disease always has the facility of occuring in a greater or lesser degree. This resistance acts like a brake so that the damage to the crop remains at a negligible or bearable level.

Does the stability of horizontal resistance, which is our main concern, have a limited duration ? We will be able to answer this question only with time. We can only suggest that a stability which does not give signs of weakening after more than ten years can probably last for a longer time and that new varieties created from parents possessing such a resistance have good chances of being equally stable for at least ten years. This is a great progress.

In spite of that Chevaugeon and Makounzi (13) (39) have shown that combined action of mutation and mitotic recombination could be at the origin of variations in the dimension of certain components of pathogen aggressiveness. Among them the aptitude for provoking lesions, the number of lesions, the sporulation intensity and toxic substance synthesis. They establish a connection between these facts and observations of Kiyosawa and Cho (33) showing differences in the response of several rice varieties to the same strain. Certain varieties oppose a better efficiency in avoiding parasite penetration, others retard better the extension of rotting, others retard or diminish the sporulation. It should not be excluded that to a change in the genetic structure controlling horizontal resistance of rice responds more or less rapidly a change of genetical structure controlling the *Pyricularia oryzae* aggressiveness. The consequence of this would be an erosion of horizontal resistance.

In any case, such erosion has not been observed in a clear way. This is a long-term risk which should not be neglected by breeders and phytopathologists, and the measures to be taken to avoid it are part of the research concerning horizontal resistance.

All these findings have led IRAT to launch itself resolutely into a research program on horizontal resistance and its exploitation. This program was developed in different directions : for measuring the level of varietal resistance it has been necessary to set up appropriate techniques ; expression of resistance and its variability are studied trying to distinguish the role of intrinsic factors of the plant and of external factors ; the genetic determinism of this type of resistance has also been tackled ; finally breeding methodology has also been defined.

This systematic approach of IRAT as well as repeated observations in the field showing the instability of resistance of certain varieties and the stability of others, are connected with the interest for horizontal resistance shown by numerous scientists, particularly those who, without having built a program around it, used it more or less empirically or began to study it by integrating it into a slightly different system (« field resistance », « slow blasting »). These last years, several international meetings have had blast as a theme, for example in the Philippines in 1979, in Brazil in 1981, in France in 1981 (28) (11) (24). The emphasis was more and more on the necessity to develop further research on horizontal resistance. An international program on horizontal resistance has been agreed upon (11).

This study is being carried out in nine countries (Brazil, Columbia, Ivory Coast, Ecuador, India, Liberia, Mexico, Nigeria, Philippines). Its purpose is to verify whether given varieties having a certain level of horizontal resistance have the same behaviour in relation to each other vis-à-vis the pathogenic population of the different environments. Another result of this experiment will be to estimate horizontal resistance level which must be attained in each of the environments. Actually one of the points frequently mentioned is the influence of the environment on the horizontal resistance of the variety. Already IRAT (30) had stressed the variability of this resistance in quite different environments and suggested that breeding should be conducted preferably by great environmental types.

While waiting for answers to these questions, which evidently will permit us to understand better the phenomena observed, verify their total or partial concordance with the theory and will probably shift the breeding strategy, we will discuss the present state of the research in the following pages ; it must be expected that mention will often be made of the results of the work of IRAT, since horizontal resistance to blast is considered there more than elsewhere as a challenge for the future.

## Methods of study of horizontal resistance

The first precautions to take in order to be able to study or to evaluate the horizontal resistance of varieties, are to exclude the effects of vertical resistance. It is essential that no confusion remains and that we do not take for good horizontal resistance a vertical resistance which shortly afterwards would disappear. The distinction is particularly difficult in the case of the rice-*Pyricularia* couple because the plant reaction and the observed symptoms are often the same for the two types of resistance. Moreover the simple qualitative observation of the symptoms (spot-type) is not enough, the horizontal resistance being a quantitative phenomenon : it is convenient to be able to use methods allowing for rapid evaluation of its level among the varieties taking advantage of its quantitative and not specific character. Finally it must also be possible to study the variability of the manifestation of horizontal resistance depending on the environmental conditions.

Different methods have been tried in the greenhouse mainly for studying horizontal resistance components and in the field to know general behaviour of the varieties in real culture conditions.

## Greenhouse tests

**The problems which** occur are the following : choice of the strain of *Pyricularia*, **choice of technique** to carry out inoculation, stage of development for inoculation of the plant, how to read the reaction ?

In Japan (18) spraying of a virulent fungus strain on seedlings at the stage of the seventh leaf has been the method used ; the varietal classification for their horizontal resistance called here « field resistance » is realized either by counting the number of lesions of susceptible types or by establishing the ratio of the number of lesions of the susceptible type to the total number of lesions. Other scientists have tried also to inoculate by injection using a strain with low aggressiveness. In spite of a certain correlation with the results obtained in the field these methods do not give sufficient representation of the resistance in real culture conditions.

IRAT confirms that inoculation by syringe can only be used to differentiate very susceptible varieties from very resistant ones ; inoculation by spraying in a growth chamber on rice seedlings (15 to 30 days) has been quite disappointing ; finally inoculation on a removed leaf which permits quick sorting of varieties resistant to some diseases for many plants gives for rice only the possibility of eliminating the susceptible material but not of comparing varieties presenting a certain level of horizontal resistance (6).

An inoculation technique by contact also called the agar slide technique, that is more precise, has been invented by IRAT (44) to measure the level of varietal resistance in standardized conditions.

The plant tested is exposed to a known quantity of spores of the fungus by application on the chosen leaf of a slide covered with agar, on which has been deposited a water suspension of spores at a determined concentration using a micropulveriser built especially for this purpose. The spore distribution is homogeneous on the slide, and therefore on the leaf. This method ensures good conditions for the germination and nutrition of the parasite without the necessity of placing the test plant in a growth chamber with a high level of humidity. The inoculation is made on the fourth leaf at the stage of semi-emergence of the fifth leaf. The number of plants to be tested by variety varies from six to thirty depending on the desired precision.

The method for reading the spots takes into account both the number of lesions per unit leaf area and the size of « efficient » lesions. The latter are those which produce most of the spores and therefore contribute most to the development of the epidemic (usually it is neither the smallest lesions with low productivity, nor the largest, which are rare). The two parameters are estimated visually, using reference diagrams.

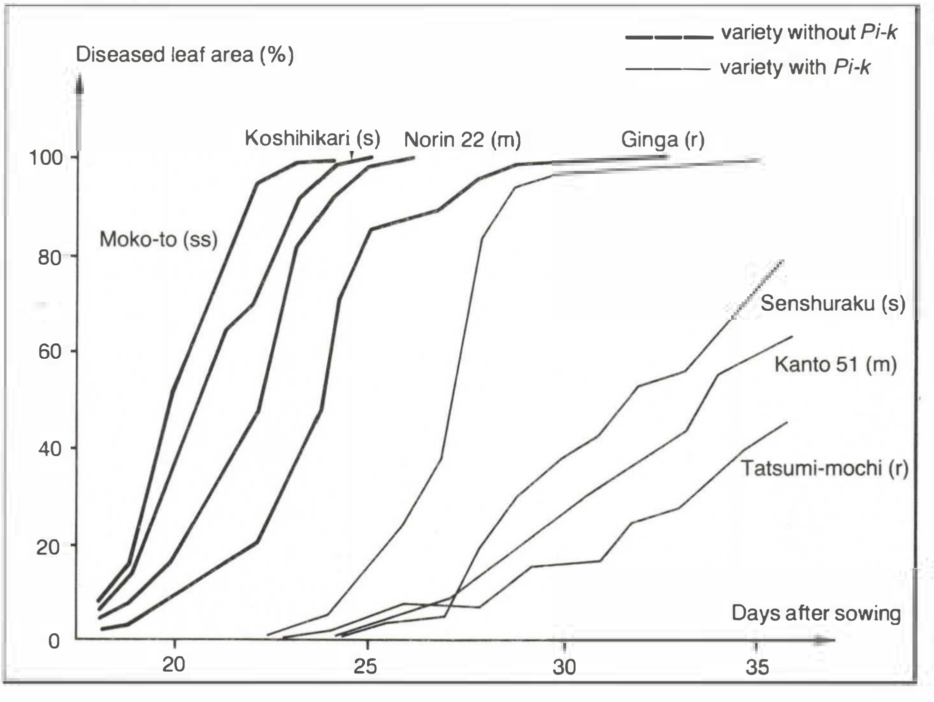
These methods for reading and these parameters concern leaf blast in particular. Some inoculation tests in the greenhouse have been made by spraying on panicles. In this case the percentage of blasted neck is measured eight days after inoculation, and again at maturity. This estimation may seem rough compared with the one used for leaf blast ; this is due to the fact that research on panicles is more recent than research on leaves ; study techniques must be perfected and we are still at the exploratory experimental stage.

## Field tests

In order to eliminate the possible effects of vertical resistance in the horizontal resistance tests carried out in the field – or more precisely in the nurseries – the Japanese research workers group the varieties in function of their vertical resistance, and make comparisons of horizontal resistance within the groups thus formed.

This may be explained by taking an example quoted by Ezuka (18) : four varieties have no vertical resistance genes, four others possess the *Pi-k* gene, as was determined by preliminary vertical resistance tests. The disease appears on the varieties temporarily protected by the *Pi-k* gene about one week after it has appeared on the other varieties (fig. 2). As it was expected, the predominance of the avirulent races of the fungus for *Pi-k* in the initial stage retarded the appearance of symptoms on the series of varieties bearing this gene. In this series it can henceforth be observed that the progression of the disease is very different from one variety to another : one is very susceptible, two have an intermediate behaviour, and the fourth is resistant, in the sense of field resistance or

*Fig. 2. The progress of leaf blast on some rice varieties with and without* pi-k *gene in the blast nursery : ss = highly susceptible, s = susceptible, m = intermediate, r = résistant – in the sense of field resistance. (From Ezuka, 1972 and 1979).*



horizontal resistance, which means that the epidemic progresses slightly and at a slow rate. The author concludes that the difference between the two groups must be attributed to vertical resistance, and that on the other hand the differences between the varieties of the group possessing *Pi-k* are of horizontal origin. From this observation he deduces that horizontal resistance (or field resistance) comparisons must only be made between varieties possessing the same type of vertical resistance.

Such tests are frequently carried out by Japanese breeders and phytopathologists, who consider that field resistance may be estimated using this method. However there is an obvious disadvantage in not being able to make comparisons between varieties without restriction.

The IBN (International Blast Nursery) method, recommended by the IRRI (cf. p. 15 ) is the most widely employed throughout the world. In practice it enables vertical resistance to be detected. It does not make possible the detection of the capacity of the varieties to reduce spore production, which is characteristic of horizontal resistance ; the spread of the epidemic is often radical and it is usually possible to sort only the varieties possessing total resistance, the others being generally classified as susceptible : the very high sowing rate only permits the analysis of leaf resistance in young plants ; finally growing conditions are very different from normal ones. For all of these reasons, the IBN method even when slightly modified, is not suited to the study of horizontal resistance.

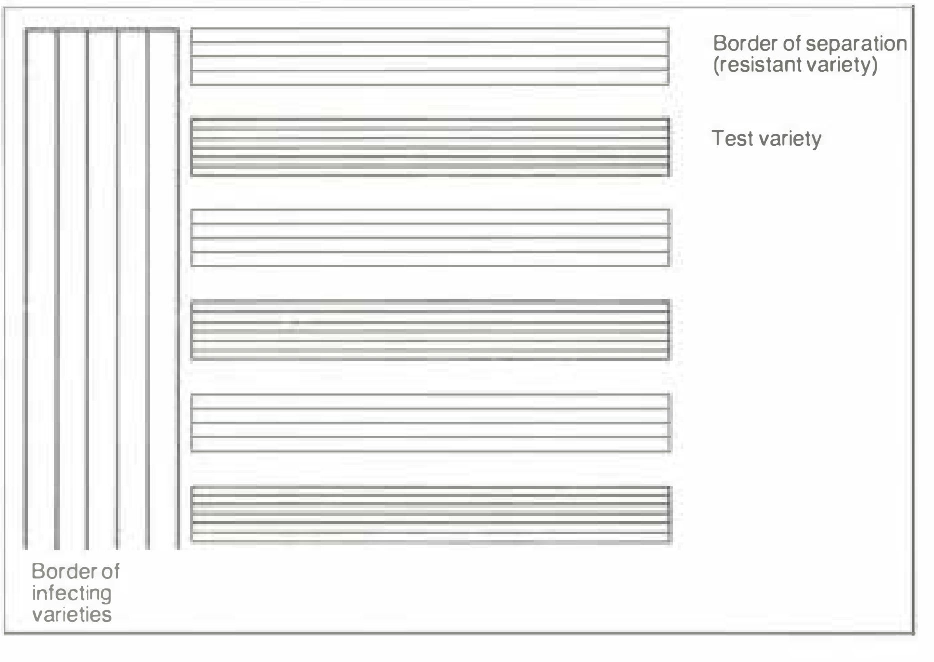
In order to overcome the disadvantages of the various above mentioned methods, the IRAT (42) has devised a test for the estimation of field resistance, known as « decreasing inoculum trial for the evaluation of resistance » or DITER trial. This method is based on the hypothesis that it is the ability of a variety to limit auto-infection that enables it to limit the spread of an epidemic in the field. The distinction must thus be made between auto and allo-infection. To do so, the progression of the epidemic is measured from the starting point of the infection, and then gradually moving away from this point.

In the DITER method, the varieties to be tested are planted in parallel plots 2 to 8 metres in length, and separated from one another by bands of very resistant varieties. At one end of this group of plots, in contact with and perpendicular to it, a border of susceptible infecting varieties is planted (fig. 3). The first inoculation is made only on the latter. It is carried out by spraying with a local strain of the parasite whose race has previously been determined on a range of differential varieties. Measures are made for each variety tested at six points, moving away from the infecting border, so that the increasing distance of the plants in relation to the source of infection produces a gradient of diminishing intensity of allo-inoculum ; therefore the influence of the border of infecting varieties, strong at point 0, is practically non-existent at the open end of the varieties tested (point 2).

Observations are made at the six points, at different times, in order to follow the evolution of the epidemic. The scoring scale is made up of ten categories (11). It is strictly quantitative, only taking into account the percentage of leaf area destroyed, which is estimated visually, with the aid of reference diagrams (fig. 4).

The score at point 0, close to the infecting border, indicates the susceptibility to allo-infection of the tested variety ; it is what could have been obtained using an IBN test. On the other hand, at point 2, the furthest away and the one we are most interested in, allo-infection is slight : if the disease develops on one variety, it means that auto-infection is high, several multiplications of the parasite occuring from lesions in this same variety, which must therefore be considered as horizontally susceptible ; a resistant variety produces little or no auto-inoculum and the disease remains very limited. The score at point 2 consequently expresses the ability of a variety to slow down the progression of an epidemic, and enables varietal differences to be revealed.

*Fig. 3 Above : varieties tested according to the DITER system (Photo Notteghem).*
*Below : diagram of the DITER system.*



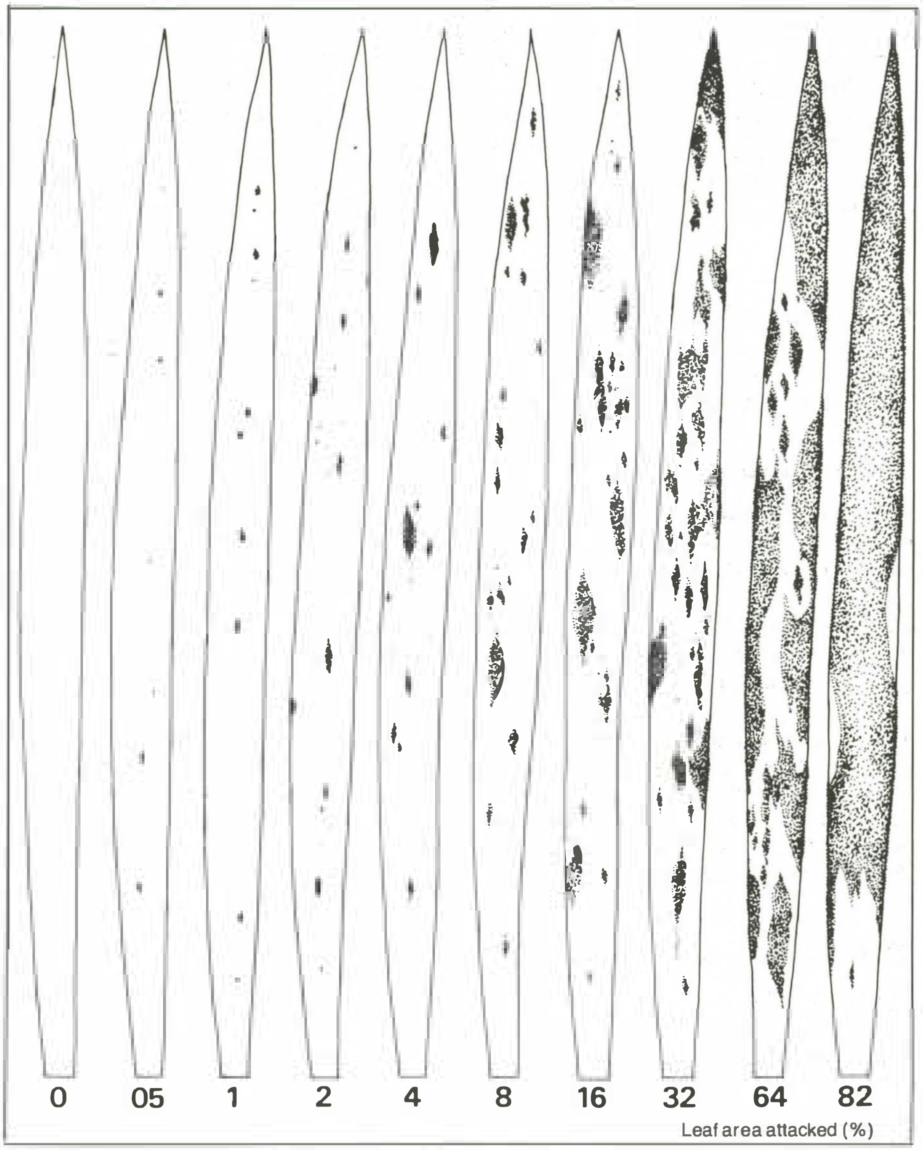



*Fig. 4 Measuring scale of % of leaf area attacked.*

The DITER trial is a good means of determining the level of horizontal resistance of lines in the course of breeding, and of the varieties. It may be employed both for leaf blast (as described above) and for neck and panicle blast. This is the trial most frequently used by the IRAT since it was developed in Madagascar in 1976. It was also adopted for international trials on horizontal resistance decided in 1981 (11), and in certain national programs, occasionally with some modifications.

The various methods that have been described for the determination and study, both in the laboratory and in the field, of horizontal resistance to blast in rice varieties, do not exclude the search for complementary information such as : the surveillance of peasant fields to be certain that there is no fall in this resistance ; the testing of varieties and analysis of the inheritance of their resistance in order to confirm that it does not have a monogenic (vertical) nature ; the more precise observation of the progression of an epidemic on large plots with a central infecting variety, etc.

## How horizontal resistance is manifested

The manifestation of horizontal resistance is not, like that of vertical resistance, an independent of environmental conditions phenomenon.

### The symptoms vary

After observing, in the Ivory Coast collections, that the leaf spots looked very different depending on the variety, the IRAT analysed the variability of leaf symptoms resulting from natural infestation in the field.

The shape and surface of the spots on leaves taken as a sample from a certain number of varieties were studied, and differences in the aspect of the spots became evident (7) :

Thus varieties such as IR 20, Tcheka-Chiao, and Dourado Precoce show typical spindle shaped lesions. On Moroberekan, Iguape Cateto and IRAT 8, the spots are large, particularly in the case of the latter, where they are very long. IR 442, on the other hand, has short, compact and irregular spots. In some varieties, the brown margin may be extended (Dourado Precoce, SE 302 G, IR 5...) ; in other varieties (IR 442) spots have one straight or almost straight margin, which could indicate that the veins or vascular bundles act as a barrier to their spreading.

### The variability factors of horizontal resistance

Is the variability of the manifestation of horizontal resistance a function of the particular characteristics of the plant ? Or does it depend on environmental conditions ? Or do intrinsic and external factors combine ?

#### Internal factors

As numerous observations made on the collections and varietal tests revealed the likelihood that levels of horizontal resistance vary according to the age of the organ and the physiological condition of the plant, it therefore appeared to be of interest to carry out more specific tests.

Several factors intervene together to cause the variation in resistance of a given organ during the life of the plant : on the one hand the « total » resistance of the latter and its variation throughout the crop cycle, and on the other hand, the particular resistance of the organ under consideration and its variation over time. Consequently it was necessary to carry out a series of tests on different organs of different varieties at different stages of development.

On the leaves the agar slide technique was employed. The results (44) demonstrated that, on the same plant, the youngest leaves are much more susceptible, and the lowest leaves almost totally resistant ; the resistance of a leaf which has just appeared increases by at least 1 to 3 in a very short lapse of time, that is about two or three days ; on the same leaf which has just unsheathed, the base part – which in monocotyledons corresponds to the growth point – is more susceptible that the end. On the other hand, the comparison between plants of different ages shows that during the early stages of growth the plant acquires a resistance which is manifested by its ability to limit the spread of the lesions : plant resistance at the 6 leaf stage is ten times greater than that of plants at the 2 leaf stage. The phenomenon of the acquisition of resistance during the early stages of growth is therefore a very important one.

The study of the resistance of other organs (23), ligule, panicular sheath and stem, and panicle show that the younger the organ the greater is its susceptibility. As in the case of the leaves, an increase in resistance can be observed with aging that is more or less pronounced and rapid depending on the organ and of course the variety.

These experiments taken together already give us a fairly general idea of the evolution of the resistance of rice in function of its stage of development : the organs have low resistance at the very beginning of their appearance, but they rapidly acquire a better level of resistance (the panicle stem may be an exception however) ; on the whole the plant attains an increasingly greater resistance as it ages, until the tillering stage, but as flowering approaches the new organs are once more very susceptible.

This variation in the resistance of the organs throughout their development, and of the plant during its cycle, means that it is necessary, in any study of horizontal resistance, to consider the epidemic in relation to the phenological stage of the plant, in order to make valid comparisons.

**External factors**

The manifestation of horizontal resistance varies not only in function of the particular characteristics of the plant, as we have seen above, but also according to the conditions of the environment in which it is placed. Water and mineral supply are two elements whose variation seems to greatly influence the manifestation of horizontal resistance. The IRAT has studied the action of water deficit, of the soil and fertilization.

**Influence of the water regime.** It is a known fact that blast is more serious for upland crops than for irrigated ones. Because of this general observation, the screening of varieties for their resistance to blast in upland conditions has long been carried out.

In Senegal (15) it has been observed on the variety I Kong Pao that blast attacks are more and more serious moving upward from the Casamance river where the rice-fields are irrigated, through the foots of slope where the crops are more or less well supplied with water depending on the level of the groundwater table, up to the Sefa plateau where rice is a strict upland culture.

Experiments (8) have been carried out in the Ivory Coast in controlled conditions, so has to ascertain the precise effect of water deficit on the resistance level of a variety, and to compare the behaviour of varieties among each other. The effect of water deficit on the gravity of the epidemic is confirmed. However in the case of a similar water deficit the varieties do not react in the same manner.

Thus, the IRAT 13 variety is more resistant to blast than the Palawan variety, which in turn is more resistant than IR 5. In the case of IRAT 13, water stress does not seem to have really perturbed the mechanism of blast resistance ; does IRAT 13 combine a greater resistance to infection than that of the two other varieties with its known capacity for drought resistance, meaning that the rice would suffer less for the same water stress ? The Palawan variety also possesses a good level of drought tolerance, and yet its susceptibility to disease greatly increases when it lacks water.

The action of drought does not only have an effect on the infection rate ; it also shortens the latency period of the disease : a variety which, in good water supply conditions would only have its first symptoms appearing ten days after inoculation, already has spots after five to seven days if it is deprived of water. The action of water deficit is all the more pronounced if it is early ; in particular, a variety which is already suffering from a lack of water before being attacked by blast does not resist as well as if the drought only occurs after the outbreak of the epidemic.

Moreover it has been observed that a large number of lesions on the leaves increases their transpiration, which accentuates the plant's water deficit (58).

At the experimental level, these results reveal the necessity of taking sufficient account of water conditions in tests for measuring horizontal resistance to blast, particularly when the tests involve a large number of varieties. Any detailed study should be carried out in precise, standardized conditions of water supply.

**Influence of soil type and fertilization.** The soil also appears to have an action in the manifestation of horizontal resistance and on its level ; this action certainly results from a complex group of phenomena not yet properly elucidated, but two cases observed by the IRAT will help understand the possible importance of this action, and will provoke questions about the mechanisms involved.

In Madagascar, in the Lake Alaotra Basin, it has long been observed (43) that blast – which is not usually a serious problem in the region, even though the main variety cultivated, Makalioka 34, is not resistant – was destroying all rice crops growing on recently cleared peaty soils. Then year after year the phenomenon decreases, until towards the fourth year the crops become normal.

In the western region of the Cameroons, whether blast is serious or not depends on the location, and it is not possible to blame differences in climate. In one place in particular, the plain of the M'Bo, it is particularly violent. Having made the assumption that probably the nature of the soil was, to a large extent, responsible for this variation, research workers set up the following device : three sites were chosen (Galim, Nyombé and the M'Bo plain) ; in each one, five varieties were tested on the existing soil and on soil brought from the two other sites, so as to eliminate other environmental effects. The varieties represented a range from strong resistance to high susceptibility.

The influence of the soil in these experiments appeared to be very important. It was quantified by giving a score to leaf blast using a scale graduated from 1 (total resistance) to 9 (total destruction of the plant). Regardless of the site, and regardless of the year, the classification of the varieties, from the most resistant to the most susceptible, remained constant. But the scores of the most resistant variety, 63-83, only vary from 1 to 3, and the losses in yield still remain negligeable ; at the other extreme, the variety 1756, very susceptible, has low losses (score 2 to 5) on the Nyombé and Galim soils, but attains 100 % (score 9) on the soil from the M'Bo plain. Consequently, the greater the susceptibility of the variety to the disease, the more the soil type is likely to influence it.

In the Cameroons, as well as in many other countries of West Africa and even in Brazil, it would seem that the soils on which the highest incidence of blast occurs are desaturated acid soils with a high C / N ratio and whose organic matter mineralises gradually. The analysis of the plants shows that these soils seem to provoke a dynamic action of absorption of mineral elements, particularly active at the beginning of the cycle, which seems to be at the origin of a nutritive disequilibrium favourable to the disease. A too great accumulation of the major elements, phosphorus, potassium, calcium, magnesium, and particularly nitrogen would occur in the plant, and would increase the susceptibility of the varieties to the extent that they do not have a high horizontal (or field) resistance. In the case of Madagascar there are soils which have just been cultivated (recent peat with a high C / N ratio) and which liberate so much nitrogen the first year that the plants have an abnormal growth and are ravaged by blast ; but in this case, as has already been mentioned, the phenomenon disappears progressively after several years.

All of these observations are naturally to be considered together with the following well-known one (49) : applications of large amounts of nitrogenous fertilizers render the rice much more susceptible to blast. Different hypotheses of interpretation have been put forward, but as yet none seems able to satisfactorily explain a phenomenon that is frequent in plant pathology.

Moreover, as the supply of soluble mineral elements in the desaturated soil does not reduce the incidence of the disease, the IRAT, relying on the observation that the « good » soils, on which blast is slight, have an intense activity which supplies to the plant mineral elements that have undergone the biological cycles of mineralisation, suggests that the influence of organic fertilization in resistance mechanisms be studied, that is the possible rôle of biological factors be evaluated (62).

To conclude dealing with soil influence on varietal resistance to blast, it must be stressed that the classification of varieties is the same for all types of soil. Even if the gravity of the disease is much greater on certain soils for varieties that are slightly or moderately susceptible, the very resistant varieties remain resistant in the worst possible soil conditions. Horizontal resistance can be effective even in ecological conditions that are favourable to the parasite.

The manifestation of horizontal resistance appears to be very variable and dependent on many external factors. When we speak of the horizontal resistance of a variety, we must specify which environment is involved. If, in the case of upland rice culture we can speak of a « habitual » environment, there are nevertheless extreme cases, for example conditions of severe drought or low nocturnal temperatures, which may perturb the growth of ill-adapted varieties and reduce their capacity of resistance. Thus it is possible to observe classifications of varieties, in the case of horizontal resistance, that differ depending on the environment.

## Relationship between leaf and panicle blast

It has gradually become apparent in the course of experiments, that horizontal resistance to leaf blast, which has been studied the most extensively up to a relatively recent date, is not necessarily linked to the resistance to panicle blast (22) (18) (1). Some varieties seem to be relatively susceptible to leaf blast and resistant to neck blast : for example, the variety IAC 25 (61). The opposite is usually the case however : for example the variety Daniela (61).

The variations in the population of the pathogen, and the variations in the environment between the leaf stage and the panicle stage, are often invoked to explain these differences in behaviour between the two stages. It is certain that all of these conditions must be made homogeneous to make it possible to check whether the genetic control of resistance is the same at both stages.

At present, numerous observations made under natural conditions are available, but as yet few observations in a controlled environment, and complementary experiments must be carried out. In the field, the DITER trial is well suited to the study of this relationship.

## Genetic determinism of horizontal resistance

The genetic determinism of horizontal resistance, certainly more complex than that of vertical resistance, has been much less extensively studied. It has simply been confirmed that this resistance was controlled by a number of minor genes, different from those involved in vertical resistance.

The IRAT has attempted to go further by analysing two series of diallel crosses, one of nine varieties in the Ivory Coast (8) (9) (38), and the other of five varieties, in Madagascar (48). The aim of these experiments was to verify the polygenic nature of horizontal resistance and to determine the heritability.

The varieties employed had two different levels of resistance, and varying geographic origins, and belonged to different genetic groups. In the series observed in the Ivory Coast, total resistance was studied, whereas in Madagascar research was concentrated on the heritability of two characteristics : the surface of efficient lesions, and the density of the lesions.

Firstly, in both of the studies, the polygenic nature of resistance was confirmed.

The study of total resistance revealed the preponderant influence of additivity on the genetic functioning of horizontal resistance, this characteristic resulting in high heritability (two separate estimates indicate 68.7 and 89.9 %). The dominance is partial and it was possible to classify the parents by order of decreasing dominance. Some varieties transmit their resistance in a very variable manner (for example 63-83), others uniformly (Moroberekan). It was also observed that the distribution of genes in the parent plants is asymetric. Finally there is no difference between the reciprocal crosses.

In the study, carried out in Madagascar, of the heritability of two specific characteristics, high heritability was observed for the density of the lesions (64 %), and moderately high heritability for the surface of efficient lesions (40 %). For both characteristics the parents may be divided into two groups : one resistant group possessing a majority of dominant genes and one group possessing a mixture of dominant and recessive genes ; as for the characteristic « lesion surface », when recessive genes are predominant, the variety is susceptible. Finally, non-allelic interactions were observed, due mainly to complementary genes.

Taken together, these results lead us, in a variety improvement program, to advocate the choice of the most resistant parents ; the risk of interaction of vertical resistance can be avoided by a detailed study of the parents and a close check of their progeny (48).

Japanese workers (18) have studied the heritability of field resistance, which we have already stated, and these workers agree, is very close to horizontal resistance, to the point that for the most part the two terms can be considered as synonyms.

This resistance is broadly of a polygenic nature : the progeny of the cross of two varieties possessing different levels of field resistance have a continuous variation of this characteristic. It happens, however, that the field resistance, mainly of upland varieties, is attributed to one or several major genes, or to groups of varied genes. The following are some examples of the conclusions of the Japanese workers :

The Yamabiko and Norin 22 varieties belong to the group that is by far the largest, in which the action of the polygenes is demonstrated. The resistance of Norin Mochi 26 is the result of the additive effect of several minor genes, two or three of which have quite a strong function ; that of Norin Mochi 4 depends on the additive effect of more than three minor genes or polygenes. The resistance of Kuroka is determined by more than three major genes, including complementary genes. As for the Chugoku 31 variety, it demonstrates a gene-for-gene relationship with the parasite. In conditions in which susceptible varieties were destroyed by the disease, it produced only a few susceptible types of lesions, and that is why it was classified in the category of field resistant varieties. It has been demonstrated that its resistance was due to a single dominant gene *Pi-f*. But later on it was severely attacked by certain strains of *Pyricularia*. We would not conclude, as do the Japanese, that this is an exception, but that this variety simply had a specific resistance which perhaps subsisted longer than in the other varieties, because, for some reason, it was not confronted with races of the parasite capable of attacking it.

Whatever the case may be, it is henceforth accepted that horizontal and field resistance of rice varieties are of a polygenic nature. In addition, data concerning the heritability of this type of resistance are now available.

## Selection methods for horizontal resistance

As knowledge about the determinism of horizontal resistance to blast has been increased, and effective tests of the measure of this resistance have been perfected, a method of selection has been defined by Notteghem (45). It is now employed in the selection centres of the IRAT. The successive operations of this method aim at verifying whether the observed resistance fulfills the criteria of horizontal resistance : stability over many years, efficiency in relation to all strains of the parasite, and non-monogenic heritability.

The success of the program naturally depends on the choice of parents. First of all the breeder chooses varieties known to have been resistant for a long time. The resistance of these parents is controlled thoroughly before they are adopted for the creation of new resistant varieties. The breeder also studies the other varieties that he wishes to use as parents for other characteristics, some of which may be susceptible to blast.

This indispensible preliminary analysis of the resistance of parents consists of a triple series of tests. Firstly, in the field, the DITER trial makes it possible to compare the resistance of varieties tested at the different levels of resistance of a range of known varieties. Secondly the test of the parents in relation to the various strains of *Pyricularia* is carried out, by means of inoculation, using a collection of local origin [1]. Thirdly, the study of the heritability of the resistance of parents aims at verifying that the latter is not governed by a dominant vertical resistance gene. To this end, in order to obtain very clear results, each resistant parent is crossed with a susceptible variety, then the plants F1 and F2 are inoculated by the agar slide method.

The varieties chosen for their resistance are crossed with agronomically satisfactory varieties, so as to incorporate into the second the polygenic systems responsible for the manifestation of horizontal resistance. The succeeding generations are tested according to methods adapted to each stage of selection.

At stage F2, bands of infecting varieties set out at regular intervals in the fields maintain epidemic conditions that are strong enough to enable effective selection to be carried out right from this phase. The scores, bearing on the percentage of plants attacked both on their leaves and at the level of their panicle stems, give an indication of the capacity of each cross to produce resistant lines.

At the following stages, that is after F3, the lines are planted at right angles to a mixture of infecting varieties with different cycles, so as to ensure a homogeneous dissemination of fungus spores over the whole of the selection field. Control varieties (one resistant, one moderately resistant, one susceptible) are placed at regular intervals between the lines, making it possible to judge the level and uniformity of the epidemic, and to decide on a score at which susceptible lines must be eliminated.

At the end of breeding, as soon as the families are homogeneous enough (F6 to F8) and their number is reduced by the selection process, the progeny retained are subjected to the DITER trial, in order to determine more precisely the level of resistance obtained.

(1) Inoculation by a collection of strains from different countries would be preferable ; this collection would have to be available in a given place. This subject was discussed during an international symposium held in Montpellier (1981) (24). At that time the IRAT already possessed samples of strains from various rice-growing regions of the world, but only limited ones.

The final procedure consists of studying the heritability of the resistance of the new varieties by crossing each one with a known susceptible variety. The aim, once again, is to ensure that the resistance observed is not determined by a monogenic system.

This selection method, although it requires numerous and varied tests, makes it possible to obtain a high level of horizontal resistance to blast, and is perfectly compatible with a simultaneous screening for other characteristics.

Another method is recommended by Buddenhagen (10), but to our knowledge it has not yet been given a practical application. Owing to its polygenic character, horizontal resistance could be obtained by means of massive recombinations requiring a maximum of crosses. Selection, carried out by means of multilocation trials would eliminate any immune variety, supposed to be vertically resistant ; the sorting of the other varieties would be effectuated according to a repeated hexagonal device, always containing a central control variety.

Finally we must point out that the CIAT (1), devoting its attention particularly to « slow blasting resistance » defined as the relative capacity of certain rice varieties to slow down the development rate of the disease even when the infection on the plants indicates susceptibility in a qualitative sense, is at present perfecting methods of selection and estimation of this resistance, whose relationship with horizontal resistance has already been stressed.

Whatever the scheme of selection adopted, a question remains : where can the best sources of horizontal resistance be found ? Buddenhagen (10) believes that the choice of resistant parents must be made in function of the ecosystem in which the improved variety is to be grown, therefore in similar ecosystems or in areas in which blast is rife, and particularly among the upland rice varieties.

Analysing the genetic variability of the *Oryza sativa* species, Jacquot (30) gives more specific information on the choice of parents.

It has already been seen that a high level of stable resistance was frequent in the traditional upland varieties of Africa or Latin America. This level would be lower on the average for the *indica* varieties grown in aquatic conditions. We are justified in wondering whether different natural selection pressures did not influence this evolution and whether in the case of aquatic rice, the intensive work of selection involved did not tend to privilege total, therefore vertical resistance, at the expense of a more stable average resistance. Whatever the case, the upland rice varieties, as a source of horizontal resistance, must be carefully studied.

What do these upland rice types represent in the *Oryza sativa* species ? Usually classified in the *indica* group, they form a group which is genetically closer to that of the *japonica* and *javanica*, varieties of aquatic or upland rice ; this group is far removed from that of the *indica* of aquatic rice.

The value of this information is that it can guide the choice of parents in cross-breeding programs : if we wish to increase the blast resistance of a variety of upland rice, the simplest method is to choose a resistant variety among the upland rice types : if the variety to be improved belongs to the *japonica* or *javanica* group, then parents from the upland rice group may also be used ; on the other hand, if an *indica* variety is to be improved, it will be necessary to devote greater attention to the difficulties inherent in cross-breeding genetically distant varieties, and in this case it may be worthwhile to cumulate partial resistance present in this type of varieties.

Resistance to blast in the main varieties of upland rice grown in West Africa and Madagascar has been studied by the IRAT and we are now quite well informed about the characteristics of this resistance. For example, three varieties will be described, one traditional African type, and the other two varieties created by the IRAT (8).

Moroberekan, one of the varieties most grown in the Ivory Coast, has always behaved satisfactorily with respect to blast, both in natural cultivation conditions and in experiments : it is often untouched by leaf symptoms, or has only a small number of spots, and the production of conidia on the lesions is usually slight or short-lived. If its resistance to panicle blast is not quite as good, it is nevertheless sufficient to avoid high loss in yield. Artificial inoculations in the greenhouse confirm a high level of resistance to infection and to the invasion of the parasite. Moroberekan, which undoubtedly has a high level of horizontal resistance, also seems to possess a gene structure of specific resistance, but which does not appear to correspond to known vertical resistance genes. This particularity would be worth verifying and explaining. Lastly, Moroberekan effectively transmits its characteristic of resistance to its progeny.

The variety IRAT 10, which results from the cross-breeding of Lung Sheng 1 with 63-104, resembles the latter in its good level of horizontal resistance to blast. It behaves equally well in the Ivory Coast, in Senegal, Mali, Upper Volta, Niger and Brazil. Artificial inoculation trials reveal a very good resistance to infection, but a relatively short incubation period for the spores which succeed in causing infection. As in the case of Moroberekan, IRAT 10 shows reactions of a differential type with certain strains of *Pyricularia*, without the involvement of a known vertical resistance gene, so that here too, a more detailed study would be desirable.

The IRAT 13 variety, obtained by mutagenesis from the 63-83 variety, has inherited and retained excellent horizontal resistance characteristics from the latter, to which are added new qualities such as its average size and its resistance to drought. In the Ivory Coast, in natural epidemic conditions, the leaf lesions, when they appear, are rare, and the neck and panicle infections are belated ; moreover, IRAT 13 greatly limits the invasions of the fungus at the level of the neck. Artificial inoculation confirms the resistance to invasion of the parasite and a very long incubation period ; it is probable that IRAT 13 has a good capacity for slowing down the production of conidia. These observations have been corroborated by other authors (66) comparing several varieties. So far no specific interactions with the parasite have been noted. The good behaviour of IRAT 13 can also be seen in other African and Latin American countries and in numerous international tests.

## For a complementary utilisation of vertical resistance ?

Research workers have imagined uniting both types of resistance, one of which, horizontal resistance, would contribute the security of a permanent level of resistance that would be as high as possible, and the other, vertical resistance, would add total if transitory resistance. A variety possessing both of these characteristics would be very attractive for the rice-growers right from the first years, and would not experience the disastrous failure of varieties with only vertical resistance.

However there are numerous difficulties involved in such an enterprise.

As it has been said, the evaluation of the horizontal resistance of a variety can only be made by excluding the effects of possible vertical resistance. Obviously, knowing which vertical resistance gene(s) a variety possesses, it is possible to carry out an inoculation with the corresponding race of *Pyricularia* and observe the degree of resistance which persists, and which would thus be of a horizontal nature. An indirect method of evaluation has been tried by Japanese workers (18) who hoped to incorporate the field resistance of one variety into the vertical resistance (*Pi-zt* gene) of another by hybridization. By taking from the F3, then the F4, plants which had not inherited the *Pi-zt* gene (those not entirely unaffected) and by testing them for their horizontal resistance, they extrapolated the level of horizontal resistance acquired by the lines which have retained *Pi-zt*.

The IRRI (20) suggests a pragmatic approach aimed at the accumulation of resistance genes, both « major » (vertical resistance) and « minor » (horizontal resistance), and which would require large scale international collaboration. The most totally resistant varieties, selected in the various programs and supposed to possess different genes owing to the diversity of the situations, would be crossed and tested on numerous sites. The repetition of the process, with the susceptible material being rejected each time, should result in the creation of varieties combining the two types of resistance.

The IRAT (3) (9) (43), along with Robinson and Japanese workers, approaches the problem from a slightly different angle. The IRAT considers it of prime importance to create varieties possessing the highest possible level of horizontal resistance, and to be absolutely certain of this level, by using the methods described above. Only at the end of selection may we consider integrating a vertical resistance gene (for example, in the case of West Africa or Madagascar, *Pi-ta*$^2$, which at present seems to be the most efficient) by means of a series of back-crosses. In this program, the variety already selected for its agronomic characteristics and its horizontal resistance is used as a recurrent parent, and at each back-cross it is necessary to check that the vertical resistance gene introduced has been conserved.

Each of these methods is both lengthy and complex.

# Other means of combating blast

# Chemical action

Chemical methods may be used to control blast, but we must stress the point that in the agro-socio-economic contexts of developing countries they may only be envisaged as one of the elements in an integrated action in which varietal resistance remains the main solution.

Research on products and methods is mainly carried out by one developed country, Japan. It is devoted essentially to irrigated rice-fields. The results obtained are transposable, with some adjustements, to upland rice. In Brazil (56) also, there has been a rapid increase in the use of fungicides to control blast, mainly on upland rice : in 1975 more than 500,000 hectares of rice were treated, whereas five years earlier the areas protected in this way did not exceed 1,000 hectares.

In the other countries producing upland rice, the use of fungicides to control blast is insignificant.

For treatment during the vegetation period, a large range of products has been tested, particularly : Blasticidin, Kasumin, Edifenphos, Benlate and Thiophanate. All of them, as well as various mixtures, are commonly employed on upland rice in Brazil (56) ; the last three have been effective in Senegal in IRAT tests (15). In Nigeria, Tricyclazole brings blast under control in only two treatments (17). Cupric compounds and mercuric compounds are excluded because of their toxic effect on plant and man. Most antibiotics (Blasticidin-S is an exception), toxic for fauna, are also excluded (49).

The utilisation of fungicide treatment in West Africa and other countries that are not very developed in their agriculture, encounters several difficulties, particularly of a financial nature.

Would seed treatment be a solution ? Tests with numerous products have so far been unsatisfactory, as their action does not continue beyond emergence. Recently a new fungicide, still under a code number, CGA 49104, has been tested by different research centres, including the IRRI and the IRAT (27) (25) : it totally protects the plant up to seven weeks, which is encouraging progress, and justifies the continuation of study.

Whatever the method of treatment and the product employed, the emergence of strains resistant to fungicides is a possibility evoked by several authors and even observed in Africa (43), which is not surprising, as this phenomenon occurs for other crops as soon as the use of chemical products becomes widespread.

# Cultivation practices

Cultivation practices likely to improve blast control are probably already employed by farmers, who have adapted them empirically, in places where upland rice-growing is a tradition. Recommendations that may be made for areas recently devoted to this crop apply to dates and rates of sowing, fertilization and some sanitary precautions. Even if we cannot expect spectacular results from their application, on the other hand the techniques recommended do not involve great expense or technicity. As these techniques must be adapted to each situation, we will only give a few very general indications.

The date of sowing must be chosen so as to enable the plant to avoid the epidemic as far as possible. A frequent case is that of such varieties as Dourado Precoce in the Ivory Coast : if maturation time coincides with the end of the wet season, the rate of blast attack is very low ; if it occurs earlier, this rate can be very high. The sowing date must therefore be determined so that maturation will correspond with the probable end of the wet season.

It is essential to avoid a too high sowing rate, as this modifies the crop's microclimate and favours a more rapid spread of the fungus.

In Brazil, in the State of Goiàs (55), for medium duration varieties, it is recommended to have rows 50 cm apart in areas where drought may be prolonged, and 40 cm apart in those where there is a more regular rainfall. The rate recommended is 50 to 60 seeds per linear metre. The earlier varieties can stand a higher rate-60 to 70. It will be noticed that wide inter-row spacing, very frequent in Brazil, is recommended primarily as a means of drought control, but it also plays a part in controlling blast.

We will only mention in passing the harmful influence of an exaggerated use of nitrogen fertilizer, which favours blast (49). Carefully calculated doses of nitrogen, phosphorus and potassium, together with possible applications of silica and other trace elements, can reduce the gravity of the disease (14).

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